

The Multilayer Nature of Ecological Networks

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Abstract

Networks provide a powerful approach to study a variety of ecological systems, but their formulation does not typically account for multiple interaction types, for interactions that vary in space and time, or for interconnected systems such as networks of species networks. The emergent field of ‘multilayer networks’ provides a natural framework for extending analyses of ecological systems to include such multiple layers of complexity, as it allows one to differentiate between and simultaneously model ‘intralayer’ and ‘interlayer’ connectivity. The framework provides a set of concepts and tools that can be adapted and applied to ecology, facilitating research on high-dimensional, heterogeneous systems in nature. Here, we formally define ecological multilayer networks based on a review of previous related approaches, illustrate their application and potential insights with analyses of existing data, and discuss limitations, challenges, and future applications. The integration of multilayer network theory into ecology offers an exciting perspective to tackle ecological complexity, with the potential to provide new theoretical and empirical insights into the architecture and dynamics of ecological systems.

Introduction

Networks provide a powerful approach to explore ecological complexity and have generated multiple insights into the understanding of the structure, function, and dynamics of ecological systems^{1–7}. Although they are fundamental to ecological theory, ecological networks have mostly been studied in ‘isolation’, in the sense of being disconnected from other networks and/or considered at a single point in space and time. Natural systems typically exhibit multiple facets of complexity: pollinators can interact with flowers in one season but not in another,⁸ and the same plant species can interact with both pollinators and herbivores^{9,10}. Despite the recognised need to move beyond the investigation of isolated, or *monolayer*, networks^{10,11} (see Supplementary Table 1), there are challenges to doing so explicitly and within a unified framework. Specific examples include the detection of community structure in networks with edges representing different interaction types¹⁰ and analysing the flow of resources in temporal networks¹².

Recent advances in the theory of *multilayer networks*^{13,14} provide a promising approach. A mathematical framework for the analysis of multilayer networks has been developed only recently, although multilayer network structures, which encode different types of interactions and/or entities as a single mathematical object, have a long history in subjects like sociology and engineering^{13,15}. The study of multilayer networks is providing new insights into diverse scientific areas^{13,14}. These advances, in concert with the growing availability of tools and large ecological data sets, provide an exciting opportunity for their theoretical and practical integration into network ecology. Here, we define ecological multilayer networks, give examples of the insights that can be gained from their application, and discuss challenges and future applications. We hope to stimulate multilayer network studies in

ecology to advance understanding of the architecture of ecological systems.

Ecological Multilayer Networks

Multilayer networks encompass two or more ‘layers’, which can represent different types of interactions, different communities of species, different points in time, and so on. Dependency across layers results from ecological processes that affect multiple layers. For example, dispersal of individuals between two patches affects the network structure of both patches¹⁶. Informally, a multilayer network consists of (i) a set of nodes, which are sometimes called ‘*physical nodes*’; (ii) a set of *layers* (each layer is an ordinary graph), which can include multiple *aspects* of layering (e.g., both time-dependence and multiple types of relationships); (iii) a set of ‘*state nodes*’, each corresponding to the manifestation of a given physical node on a specific layer; and (iv) a set of (weighted or unweighted) edges to connect the state nodes to each other in a pairwise fashion. The edge set includes both *intralayer* edges (i.e., the familiar type of edge) and *interlayer* edges, which connect state nodes across layers. See Box 1 for a formal definition and Fig. 1 for a detailed example of an ecological multilayer network.

Previous studies of ecological multilayer networks (see Supplementary Table 1) have for the most part used multiple but independent networks of the same system, with interlayer edges formally absent. In such cases, network diagnostics are calculated independently for each layer, and the resulting values are then applied in subsequent analyses. For instance, Olesen *et al.*⁸ reported—using a plant–pollinator system sampled over 12 years and represented with 12 individual networks—that connectance (i.e., edge density) exhibits little variation over time despite significant turnover of species and interactions. Here, we focus on networks with explicit interlayer con-

nectivity, which enables one to ask questions about interactions between the processes that operate within and among layers. To set the stage for the use of multilayer networks in ecology, we first identify the major types of layering that are relevant for ecological systems (see Fig. 2 and Supplementary Table 1).

Layers Defined Across Space or Time

Early work on spatial and temporal networks focused primarily on how the composition of species changes in time (e.g., across seasons) or over environmental gradients, especially in food webs^{17–20}. More recent studies have focused on studying spatial and temporal dissimilarities in species and interactions^{21–23}. This variability finds a natural representation in multilayer networks: one can define a monolayer network at each point in space or time, and then use interlayer edges to connect each node to its counterparts in different layers. Layers in temporal multilayer networks are typically ordered (‘ordinal coupling’; see Fig. 2a), but the order of the layers is not important for spatial networks (‘categorical coupling’; see Fig. 2b). Another approach is to use a network of networks. For example, Gilarranz *et al.*¹⁶ defined a spatial network of plant–pollinator networks in which each community of plants and pollinators is a layer and in which interlayer edges represent species extinction and colonization. By considering a network of layers (see the inset of Fig. 2f), whereby each layer was construed as a node, the authors demonstrated an association between the importance of communities (quantified using a measure of node betweenness centrality) and their architecture: communities with higher betweenness in the network of layers are also more nested, with potential consequences for the stability of the communities^{24,25}.

Layers Defined by Interaction Type

Because the stability and function of ecological networks can depend on the way in which different interaction types are combined in communities, considering only a single interaction type can give an incomplete picture of system properties^{10,11,25–29}. For instance, Bastolla *et al.*²⁶ illustrated that both the structure of mutualistic networks and competition for common resources can determine the number of co-existing species in a system. Some ecological networks have a common set of species (e.g., a set of plants connected to their pollinators and herbivores⁹). One can represent such data^{9,30,31} in a multilayer formalism using a ‘diagonally coupled’ multilayer network (see Fig. 2c). Each ecological interaction occurs in a different layer, and inter-layer edges connect common species to their counterparts in the different layers.

Another approach is to examine different interaction types between all species in a system using ‘node-aligned’ multilayer networks, in which all entities exist on all layers^{29,32,33} (see Fig. 2d). Kéfi *et al.*²⁹ used a highly-resolved ecological community from the central intertidal coast of Chile to construct a multilayer network in which each layer consists of all 104 species but represents different interaction types: trophic, non-trophic positive (e.g., refuge provisioning), and non-trophic negative (e.g., predator interference). They found that the distribution of non-trophic edges throughout the food web was different than what would be expected by chance (by reshuffling the non-trophic edges while fixing the trophic web), suggesting that there is a strong association between the different layers of the network. Such structural patterns suggest the possibility of important dynamic constraints on the combined architecture of trophic and non-trophic interactions²⁹.

Layers Defined by Different Group Identity

An intuitive way to describe and examine variation in individual-based interactions between populations of the same or different species is with an interconnected network in which each node appears only in one layer (see Fig. 2e). In disease ecology, this representation models interpopulation or interspecific disease transmission (when each layer is a population of a different species), while considering an underlying social network³⁴. For example, intralayer edges can represent the social structure of bat groups, and interlayer edges can represent a vector-borne disease that can be transmitted among these populations. Moreover, interconnected networks are not limited to individual organisms. For example, one can define a multilayer network in which each layer represents a food web (with its own trophic interactions), and interlayer edges represent trophic interactions among species from different food webs^{35,36}.

Layers Defined by Levels of Organisation

Biological processes at any given organisational level (e.g., genes, individuals, populations, etc.) can depend on processes at other levels³⁷. For example, changes in species' biomass can affect the stability of food webs in dynamical models based on allometry³⁸. When the layers in a multilayer network represent different levels of organisation, one has a 'multilevel' network, and interactions among nodes at a lower level automatically impose interactions at upper levels¹³. For example, a trophic interaction between two species from two different patches entails an interaction between the patches. The simplest example is a 2-level multilevel network, which can also be construed as a network of networks (see Fig. 2f). In an analysis of a 3-level multilevel network (population, community, and metacommunity),

nity), Scotti *et al.*³⁹ illustrated that the metacommunity was sensitive to population-level processes (e.g., social dynamics) that cascaded through the different levels. The identification of such dependencies emphasizes the value of a multilayer approach.

Analyses of Ecological Multilayer Networks

To illustrate the kinds of insights that can be gained from taking a multilayer approach we study example ecological multilayer networks in which layers are explicitly connected. We consider (1) modularity, a structural property that is commonly studied in monolayer networks, and (2) extinction cascades, a consequence of structure that is common in robustness analyses of networks. We use both synthetic networks and networks constructed from empirical data.

Modularity

In monolayer networks, modularity quantifies the extent to which a partition of a network is organized into groups (modules) of species that interact more strongly with each other than with other species^{40,41}. To our knowledge, modularity has not yet been explored in ecological networks that incorporate interlayer connectivity. To illustrate the distinction between studying a multilayer network and studying a collection of multiple networks, we start with a synthetic example from Fontaine *et al.*¹⁰. In this example, a plant–herbivore network and a plant–root–parasite network interconnect via a common set of species, which are the plants (see Fig. 3a). Interlayer edges connect each plant species to its counterpart on the other layer (see Figs. 2c and 3c,d). Thus, each plant appears in both layers and has two instances corresponding to different ‘state nodes’, which can be assigned to different

modules (see Supplementary Note 1 for details on how we calculate multi-layer modularity and assign state nodes to modules). The propensity of a state node to belong to distinct modules depends on the relative weights of interlayer and intralayer edges^{42,43}. Ecologically, it depends on the extent to which processes in one layer affect those in the other. To develop our argument, we consider three conceptual scenarios:

1. When the *interlayer edge weights* are 0, the two networks are independent entities. The instances of plants in different layers must belong to different modules, and modules are defined separately for herbivory and parasitism. Hence, herbivory has no effect on parasitism (and vice versa), and no perturbation can pass from one layer to another (see Fig. 3b).
2. At the other extreme, *interlayer edge weights are much larger than intralayer ones* (and they are infinite in the limiting case). In this scenario, herbivory and parasitism always affect each other. This need not imply that each plant will always be parasitized and preyed upon, but herbivory does always render plants more susceptible to parasites, and vice versa. Consequently, each of the two instances of a plant always belong to the same module. Note that modules can contain species from any of the three guilds and from either interaction types (see Fig. 3d).
3. *Interlayer and intralayer edge weights have comparable values* (i.e., they are on similar scales). In this scenario, herbivory has some effect on the propensity of a plant to be parasitized, and vice versa. A plant can therefore interact strongly with a given set of herbivores in one layer and with a given set of parasites in another. Each of the

two instances of a plant can belong to different modules. Modules can contain species from any of the three guilds and either interaction type, but the identity of the modules can be rather different from those in the previous two cases (see Fig. 3c).

This example illustrates that defining community organisation in multilayer networks depends strongly on the extent to which the ecological processes that operate in the different layers affect each other (in our example, the relationship between parasitism and herbivory). Another insight is that considering intermediate values of interlayer edge weights provides a possible means to identify the plants that can buffer perturbations, specifically those for which the two instances are assigned to different modules (see Fig. 3c).

Several studies outside of ecology have illustrated that modular (and other mesoscale) network structures can change over time^{42,44,45}. In ecology, such network variation was considered in a study based on the analysis of multiple disconnected networks⁴⁶. Time-dependent modular structure, including changes in module composition over time, can also be examined by studying a single mathematical object that describes a single time-evolving community. As an example, we consider a network representing the infection of 22 small mammalian host species by 56 ectoparasite species during six consecutive summers in Siberia (1982–1987)^{47,48}, yielding a multilayer network with 6 layers. We quantify intralayer edge weights as the prevalence of a given parasite on a given host, and interlayer edge weights as the relative changes in abundance between two consecutive summers (see Fig. 2a, Supplementary Fig. 1, and Supplementary Note 3). This results in interlayer edge weights that are on a similar scale as intralayer edges and which are also non-uniform. To our knowledge, non-uniform interlayer edge weights have not been explored in published applications of multilayer modularity

maximization.

In a temporal network, a given species can interact strongly with some species at one time point and with other species at other times. Consequently, each state node can belong to a different module at different times, and modules can vary in size over time^{42,43}. We define ‘host adjustability’ and ‘parasite adjustability’ as the proportion of hosts and parasites, respectively, that change module affiliation at least once. We observe non-negligible host and parasite adjustability: about 47% of the hosts and about 35% of the parasites change their module affiliation at least once (see Supplementary Fig. 2), and module sizes also change significantly over time (see Fig. 4).

Constructing and analysing a temporal network also allows one to consider hypotheses regarding the effect of intralayer and/or interlayer connectivity on community structure (see Supplementary Note 3). For example, to test the hypothesis that the observed modular structure depends significantly on the identity of hosts and parasites that change in abundance, we reshuffle the interlayer edges between each pair of consecutive layers. We find that the observed network has higher maximum modularity than the reshuffled networks ($\overline{Q}_B^{\text{observed}} \approx 0.55$ versus $\overline{Q}_B^{\text{reshuffled}} \approx 0.21$, $P < 0.001$; see Supplementary Table 3). Additionally, the observed network has approximately 6 (respectively, approximately 15) times fewer modules than when reshuffling the order of interlayer edges of hosts (respectively, parasites), and all hosts and parasites switch modules at least once in the reshuffled networks (see Supplementary Table 3).

These results point to strong temporal effects in the organisation of the ecological community which may be incompletely assessed by studying each layer separately or by aggregating all species and interactions (see Supplementary Note 3). On one hand, if one does not aggregate temporal layers,

interlayer edges may appear only very sparsely, which can prove very challenging for network analysis. On the other hand, data aggregation entails a set of underlying (and usually implicit) assumptions^{13,49}, and different aggregation methods can lead to qualitatively different conclusions. In contrast, multilayer networks lend themselves naturally to address questions about time-dependent phenomena^{12,42–44}. Temporal variations in the size and composition of modules may be relevant to phenomena such as species coevolution, coexistence, and community stability^{4,10,50}. In our example, hosts assigned to more than one module may provide important bridges for transmission of ectoparasites across years and/or modules. These hosts can change their ecological function in the system⁴⁸, and such flexibility in community structure may contribute to system robustness in the face of perturbations.

Robustness to Perturbations

Network structure affects (various forms of) stability^{7,24,25}. To illustrate how multilayer networks can contribute to studies of stability, we use a network with two layers, plant–flower-visitors and plant–leafminer-parasitoids³⁰, that are interconnected via the same set of plants (see Fig. 2c and Supplementary Note 4). We consider parasitoid extinction in two scenarios: (1) direct secondary extinction by plant removal; and (2) tertiary extinction in which removal of pollinators causes plant secondary extinction that, in turn, results in parasitoid tertiary extinction (see Supplementary Table 4). We find that parasitoid extinction occurs more slowly in the multilayer network than in the monolayer network (see Fig. 5). In scenario (2), we allow independent plant extinctions on top of the removal of flower visitors. This results in non-trivial extinction patterns in which the outcome depends on the probability

of independent plant extinctions. When the probability is low, the dynamics resemble those of the tertiary extinctions in the multilayer network. When the probability is high, extinctions occur for a smaller proportion of removed species (see Fig. 5). Therefore, considering the multilayer nature of the network changes the qualitative conclusions about the robustness of parasitoids to extinctions. There are many ways to extend this kind of analysis (e.g., see Supplementary Note 5), and studying such scenarios should be valuable for improving understanding of the interplay among different interaction types and their effect on system robustness.

Future Directions and Applications

As our review of recent network studies and analyses demonstrate, multilayer networks provide a versatile and powerful framework for investigations in community ecology. This is also true for biogeography, where networks that include species dispersal or colonization/extinction dynamics as interlayer edges can help one understand how spatial dynamics affect community structure and stability¹⁶. A multilayer formalism can address not only correlations between geographic distance and beta diversity of species/interactions (which to date have been studied using multiple disconnected networks; see, e.g., Trøjelsgaard *et al.*²³), but also the mechanisms behind such correlations. Another open area concerns the effect of space on the stability of ecological communities⁵¹. In such an application, one can use a multilayer network, which explicitly incorporates different instances of the same species at different locations, in place of the matrix of interactions for a single community in space when examining system stability^{24,28}. Habitat alteration is a growing concern, and it would be interesting to explore the stability of ecological networks with different spatial connectivity patterns (encoded in

the interlayer edges).

One can use a temporal food web to explore bioenergetic flows across food webs—an area that remains largely unexplored¹². Layers can represent temporal instances of a given food web, and interlayer edges can represent changes in species biomass with time. It is also possible to study spatial structure in resource flow in interconnected food webs, such as those of lakes or ponds that are interconnected via common sets of animals³⁶. Another key question in food-web theory is the effect of parasitism on food-web structure and stability^{52–54}. For example, parasitism may have different effects than trophic interactions on a given species. Parasitised hosts can be more susceptible to predation, but it is unclear how the structure of host–parasite networks affects the trophic interactions between hosts. One way to model such systems is by coupling a host–parasite network and a food web (see Fig. 1).

In disease ecology, multilayer networks provide a possible means to analyse disease transmission when there are multiple hosts and parasites^{34,55}, which to date remains a difficult scenario to analyse. In movement ecology, multilayer networks can help model the relationship between a network of social interactions and a network of movement patterns to understand moving decisions. In animal behaviour, one can explore networks in which intralayer edges between individuals represent reproduction and interlayer edges represent movement (and hence gene flow) to study genetic relatedness among individuals as a function of both dispersal and within-group social behaviour.

In conservation biology, one can model different connectivity scenarios using a multilayer network in which each layer describes the movement patterns of a different species. This can inform decision-makers on which

land-use designs are best-suited for the movement of a diverse set of species. Multilayer networks can also help improve the identification of keystone species. A simple definition is one based on calculating a centrality measure of the species in a food web (i.e., keystone species have the highest values of that centrality)⁵⁶. A more nuanced definition of centrality, and hence of keystone species, can incorporate participation in several interaction types as well as temporal and spatial dependencies.

Importantly, ecological multilayer networks can help us address many other questions, and we present some of them in Supplementary Table 1.

Limitations and Challenges

Naturally, the use of multilayer networks should be contingent on the formulation of a problem, and one needs to consider whether using monolayer networks is more appropriate. The collection of the necessary data for studying questions with multilayer networks may be resource-intensive, because data would need to be gathered in multiple places, at multiple times, and/or with different observational methods to capture different types of interactions. Measuring interlayer edge weights may require additional sampling efforts that are different from those used for collecting data on intralayer edges. Fortunately, many data sets already exist (see Supplementary Table 1), and these can potentially be explored as multilayer networks, but these data are scattered in the literature and need to be curated.

It is not always clear how to define interlayer edges, and the choice of definition can play a significant role in analyses. For example, interlayer edges that connect species in two different communities may relate to species dispersal or changes in a species' state (e.g., abundance). Moreover, intralayer and interlayer edges can represent ecological processes at different scales,

and different types of interactions may involve different ‘currencies’. For example, pollination is measured differently than dispersal, and it is important to consider discrepancies in the scales of the two edge types. Nonetheless, to explore questions about variation across space, time, or different interaction types, data about both intralayer and interlayer edges are necessary regardless of whether one uses a multilayer approach.

As with previous advances in network ecology, one can borrow and adapt methodological techniques from the more general science of networks^{2,4,50,57,58}. Although a natural first step is to adopt (and adapt) diagnostics and algorithms from the many that are available in applications of multilayer networks to other disciplines^{13,14} (see Table 1), it is important to determine which existing methods are best suited for ecological applications, and it is even more important to develop methods and diagnostics with ecology specifically in mind. These include multilayer versions of common network diagnostics (e.g., vulnerability and generality), null models to test hypotheses about network structure⁵⁹, and mathematical models for dynamical processes. Availability of software^{50,60,61} has played an important role in the accessibility of monolayer network analyses, and it is equally important to implement methodology in easy-to-use tools to visualise and analyse ecological multilayer networks. Several software packages are already available (see Supplementary Table 5), but these are not yet as mature as those for monolayer ecological networks.

Conclusions

Although ecological systems have multiple layers of complexity, they are not usually analysed as multilayer networks. The simultaneous expansion in the availability of both ecological data and tools to analyse multilayer

networks^{13,14,55,62} provides a timely and exciting opportunity for ecologists to explore the multilayer nature of ecological networks. The strength of a multilayer approach is the ability to formulate and analyse networked systems in a way that explicitly encompasses processes that operate both within and among layers (and the interaction between these processes). This bestows new and multiple ways to model systems, enabling new insights into the processes that yield network structures. Working within a given framework also facilitates comparisons of results across ecological systems and network types because of the consistency in technical terms and methodology. A unified framework further encourages collaboration with scientists from other disciplines, facilitating the advancement of multilayer network ecology. Other fields of study can, in turn, benefit from methodology and theory that is developed for ecological multilayer networks, as has happened with monolayer ecological networks⁶³. The integration of multilayer network theory into ecology offers an additional perspective to tackle ecological complexity, with the potential to provide new theoretical and empirical insights into the architecture and dynamics of ecological systems.

Data and Code

Data for the temporal network can be found in: [10.6084/m9.figshare.3472646](https://doi.org/10.6084/m9.figshare.3472646). The code for general procedures to prepare data, manipulate networks, post-process modularity calculations, and analysis of network robustness was written in R and can be found in: ([10.6084/m9.figshare.3472664](https://doi.org/10.6084/m9.figshare.3472664)). The code for examination of modular structure was written in MATLAB ([10.6084/m9.figshare.3472679](https://doi.org/10.6084/m9.figshare.3472679)).

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Author contributions

S.P. conceived the idea, performed numerical simulations, and analysed the data; M.A.P contributed insights about the mathematics of multilayer networks and data analysis; and M.P. and S.K. contributed insights about the use of multilayer networks in ecology and interpretation of results. All authors wrote the manuscript.

Competing financial interests

The authors declare no competing financial interests.

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Display items

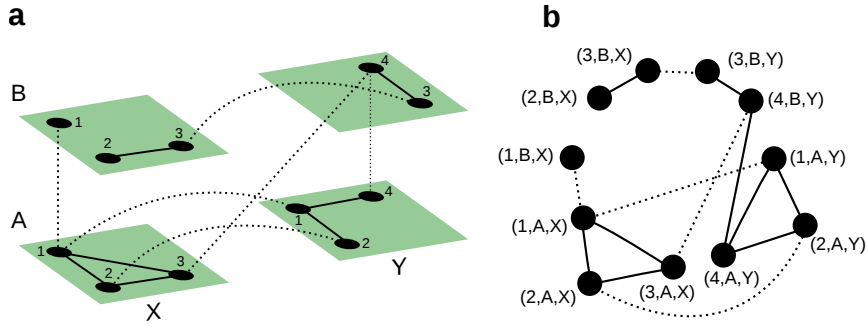
Box 1. Definition of Multilayer Networks

A *multilayer network* is a quadruplet $M = (V_M, E_M, V, L)$, where the set of entities (i.e., physical nodes) is V , as in ordinary networks, but there are several ‘aspects’ of layering, such as different interaction types, different points in time, different patches in space, and so on. An ‘elementary layer’ is a single element in one aspect of layering (see the figure in this box), such as a single point in time or a single type of relationship. As we illustrate in the figure, a ‘layer’ encompasses one choice of elementary layer for each type of aspect. We include such relationships using sequences $\mathbf{L} = \{L_a\}_{a=1}^d$ of sets L_a of elementary layers, where a indexes the d different aspects. Note that $d = 0$ for an ordinary network, $d = 1$ when there is one type of layering (e.g., as in multiplex networks), and $d = 2$ when there are two types of layering (e.g., a network that is both multiplex and time-dependent). The set $V_M \subseteq V \times L_1 \times \dots \times L_d$ of node-layer tuples (i.e., state nodes) encodes the manifestations of an entity $v \in V$ on a particular layer $l \in \hat{L} = L_1 \times \dots \times L_d$. The edge set $E_M \subseteq V_M \times V_M$, which includes both intralayer and interlayer edges, encodes the connections between pairs of state nodes. In a given layer, the intralayer edges encode connections of the specified type (e.g., a certain type of interaction at a given point in time). Interlayer edges can connect the same physical node either to one of its counterparts on a different layer through a so-called ‘diagonal’ edge or to a different physical node on a different layer.

To illustrate the above notions, consider a space-dependent multiplex network, which has $d = 2$ aspects of layering. In such a network, one aspect is multiplexity (i.e., the different types of ecological interactions), and the

other is space. The elementary layers are given by a set of relationships (e.g., A or B , so the elementary-layer set is $L_1 = \{A, B\}$) or a set of patches (e.g., X or Y , so the elementary-layer set is $L_2 = \{X, Y\}$), and a layer consists of a tuple of elementary layers. For example, the intralayer edge between nodes 2 and 3 in layer (B, X) encodes a relationship of type B at patch X between these two nodes. A function $w : E_M \rightarrow \mathbb{R}$ yields weights on edges. A pair of node-layer tuples, (u, α) and (v, β) , are adjacent if and only if there is an edge between them. Thus, one places a 1 in the associated entry in an adjacency tensor (a generalisation of a matrix that consists of a higher-dimensional array of numbers)^{13,15} if and only if $((u, \alpha), (v, \beta)) = 1$. Otherwise, one places a 0 in the corresponding entry. Note that one can ‘flatten’ such an adjacency tensor into a matrix, called a ‘supra-adjacency matrix’, with intralayer edges on the diagonal blocks and interlayer edges on the off-diagonal blocks (see Fig. 1b).

Constraints on this general definition restrict the structure of a multilayer network¹³. For example, ‘diagonal coupling’ (see Fig. 2c) is a constraint in which the only permissible type of interlayer edge is one between counterpart entities on different layers. In a ‘node-aligned’ network, all physical nodes occur in all layers (see Fig. 2d). See¹³ for additional definitions, discussions of relevant concepts, and important types of constraints on M that produce common types of multilayer networks.



Toy example of a multilayer network. **a**, This multilayer network has two aspects: one with elementary layers A and B , and the other with elementary layers X and Y . The layers are (A, X) , (B, X) , (A, Y) , and (B, Y) . An example of a diagonal interlayer edge is the edge between node 1 on layer (A, X) and node 1 on layer (B, X) . **b**, The graph (a so-called ‘supra-graph’) that corresponds to the multilayer network in panel (a). Each node in this graph is a node-layer tuple (i.e., a state node) in the corresponding multilayer network. For example, the aforementioned diagonal interlayer edge is the edge $((1, A, X), (1, B, X))$, and the intralayer edge between nodes 2 and 3 is $((2, B, X), (3, B, X))$. Intralayer edges and interlayer edges are given, respectively, by solid and dashed arcs. [This figure is modelled after Fig. 2 of Kivelä *et al.*¹³.]

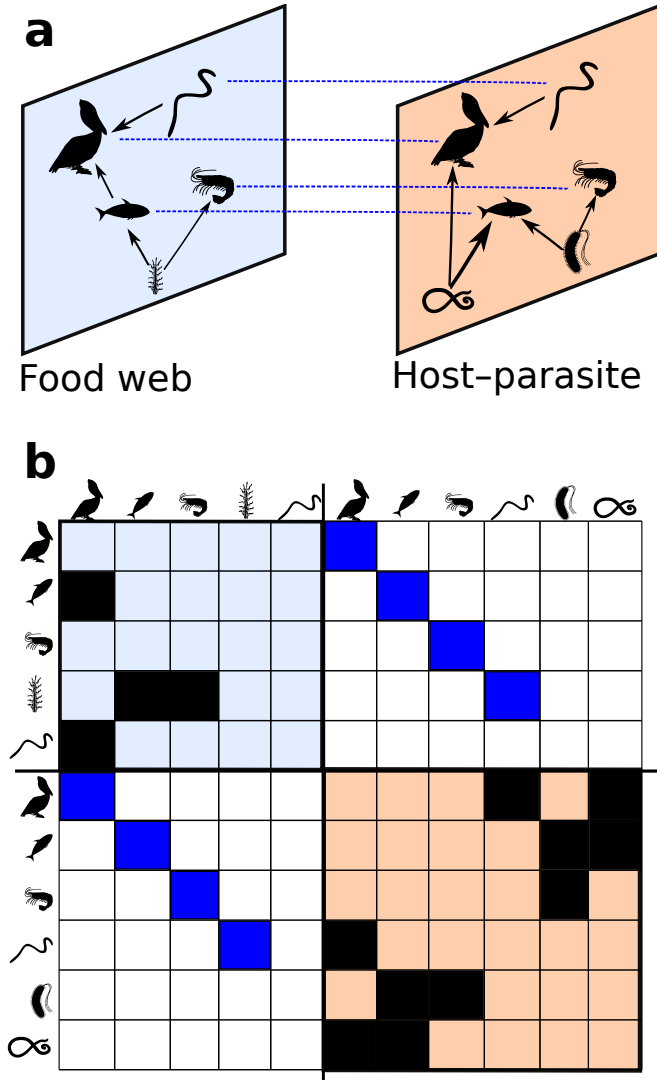


Figure 1: An ecological multilayer network with two interaction types. **a**, The network depicts an aquatic food web (light blue layer) and a host–parasite network (light orange layer). Species that occur in both layers are interconnected with dashed blue interlayer edges. Note that one parasite appears in both layers and can therefore play a role as a prey and/or a parasite for the pelican. **b**, A supra-adjacency representation of the network in panel **a**. Coloured blocks correspond to the network layers. Intralayer and interlayer edges, respectively, are black and blue matrix cells. Species that appear in two layers also appear twice in the matrix. These are ‘state nodes’ of the same physical node.

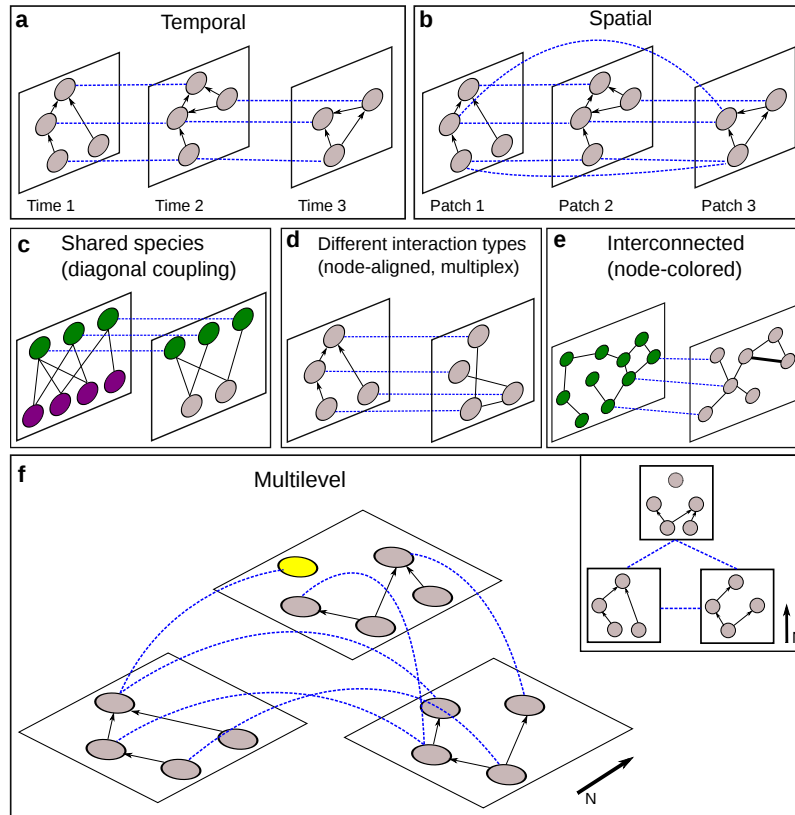


Figure 2: Multilayer networks in ecology. In these toy examples, layers are squares, solid black lines are intralayer interactions, and dashed blue arcs are interlayer edges. **a**, Temporal food webs. Nodes are connected to themselves across layers in an ordinal way (one layer follows another). **b**, Spatial food webs. Nodes are connected to themselves across all layers (i.e., categorical interconnections). In panels **a** and **b**, it is permissible for species or intralayer interactions to appear in one layer but not in another. **c**, Networks with different interaction types that are connected through shared species. Layers are ‘diagonally-coupled’, so interlayer edges occur only between shared species. **d**, One can represent different interaction types among a given set of species (e.g., trophic and facilitative) using a node-aligned multiplex network, in which all nodes appear in all layers and each layer corresponds to a different interaction type. Nodes are connected to all of their counterparts across layers. **e**, Two interacting populations of different hosts. Nodes are individuals, and intralayer and interlayer edges are, respectively, social ties within and between populations. In this example, each node appears in one layer. **f**, A multilevel network representing a metacommunity. Layers are communities, and nodes are species. Intralayer edges are trophic interactions, and interlayer edges represent species dispersal among communities. A species can also disperse to a new community (represented by the yellow node). Communities are often embedded in space (e.g., different habitats or patches). In the inset, we illustrate that such networks are sometimes represented without explicit specification of interlayer edges. Interactions among species at a lower level automatically impose interactions among the communities.

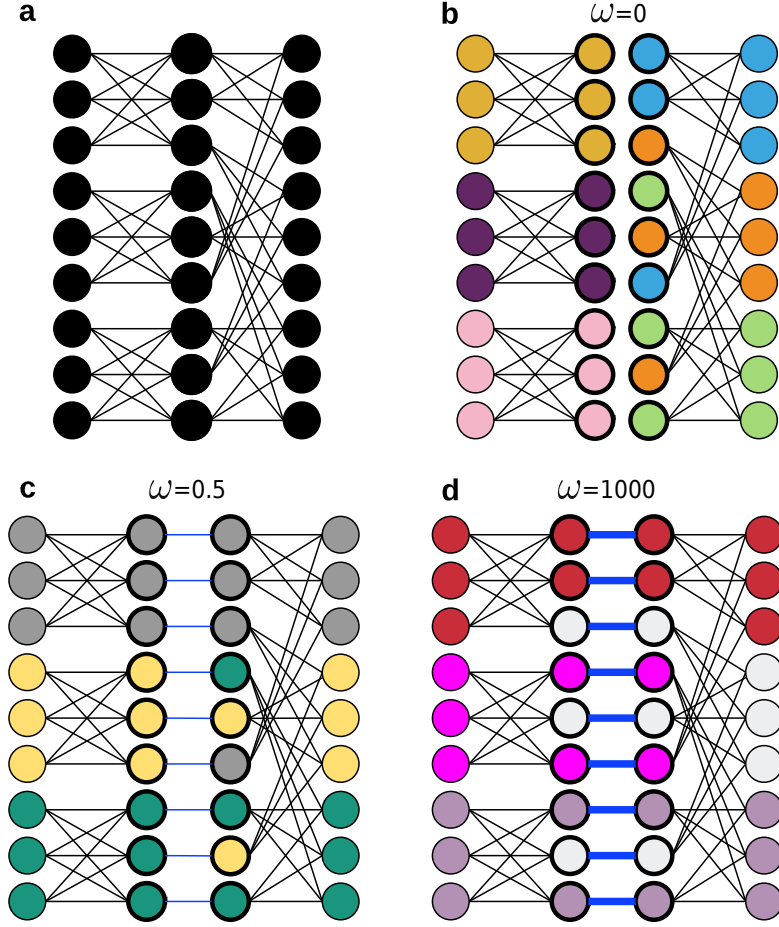


Figure 3: Modularity maximization in a diagonally-coupled multilayer network. **a**, The example network from¹⁰ that does not have interlayer edges. In **b**, **c**, and **d**, the network has two layers, which interconnect via a common set of nodes (with thick borders). Interlayer edges (in blue) connect the two instances of a node. In panels **b**, **c**, and **d**, we test three different scenarios. In each panel, nodes of the same colour belong to the same module. We construe the left set of nodes as the root-parasite guild, the middle set with thick borders as plants, and the right set as herbivores. For our calculations, we use $\omega = 1000$ to represent interlayer edge weights of ∞ . In panel **b**, we obtain maximum modularity of $\bar{Q}_B \approx 0.667$, each layer has 3 modules, and no plant state nodes appear in the same module. In panel **c**, $\bar{Q}_B \approx 0.651$, and the network is partitioned into a mean of $\bar{n} \approx 3.04$ modules. On average, 4.6 (i.e., approximately 51%) of the plants are assigned to more than one module. In panel **d**, $\bar{Q}_B \approx 0.99$, and we obtain a mean of $\bar{n} \approx 3.38$ modules, and state nodes of each plant belong exclusively to a single module. See Supplementary Notes 1 and 2 for details about our calculations.

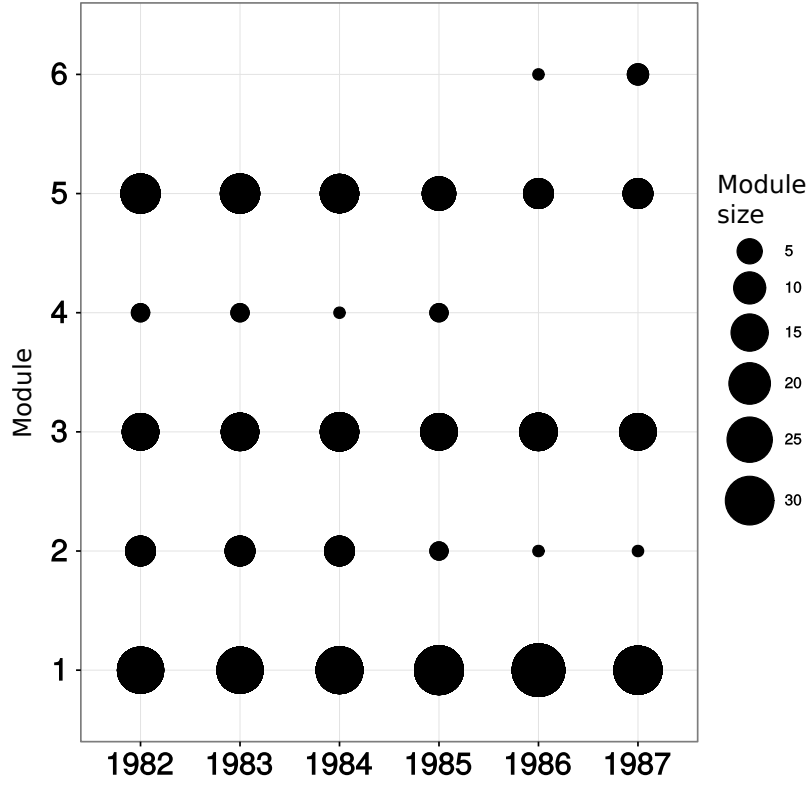


Figure 4: Yearly variation in module size. We examine modular structure in a network representing the infection of small mammalian hosts by fleas and mites. Because species can switch modules across years (i.e., across layers), we observe variation in module size. For example, module 1 maintains a relatively large size across years, whereas module 4 exists only in four of the six layers. This figure depicts a particular instantiation of the 100 runs of the modularity-maximization algorithm (matching the run in Supplementary Fig. 2) that represents the run with the maximum value of the maximum modularity. See Supplementary Note 1 for details about our calculations.

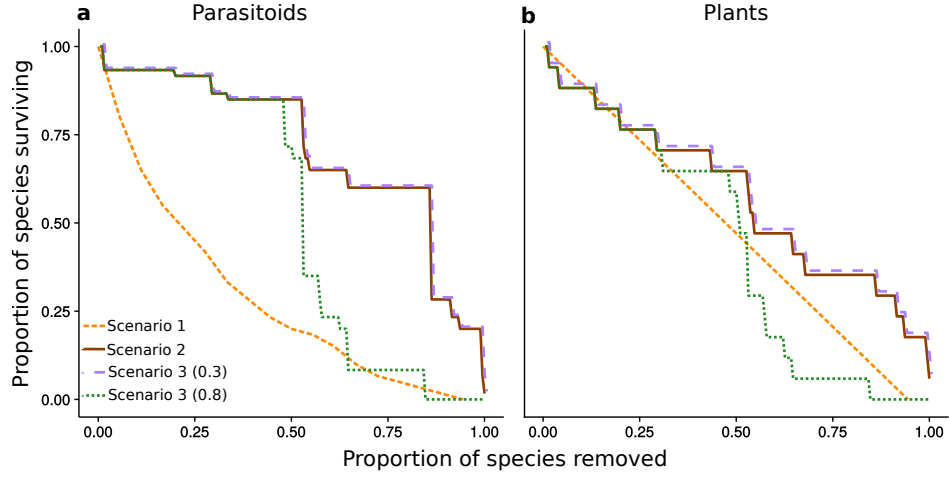


Figure 5: Network robustness to species removal in a multilayer network of plant–flower–visitors and plant–leafminer–parasitoids. The proportion of surviving (a) leafminer parasitoids and (b) plants as a function of the proportion of species removed in three scenarios. In scenario (1), we remove plants from the plant–leafminer–parasitoid layer (orange curves). This is a reference scenario of the monolayer network; plant removal is linear in the proportion of species removed. In scenario (2), we remove flower visitors and quantify secondary extinctions (the proportion of surviving species) in plants and concomitant tertiary extinctions of leafminer parasitoids (brown curves). Scenario (3) is the same as (2), but with additional plant removal (which is independent of the secondary plant extinctions), with probability 0.3 (purple curves) or 0.8 (green curves). We detail the algorithms for each of the removal scenarios in Supplementary Table 4. Note that the curves for scenarios 2 and 3 with low probability overlap and so were slightly separated for clarity.

Table 1: We list a selection of diagnostics for, and other features of, multilayer networks; and we give example applications of these diagnostics and features for ecological multilayer networks (EMLNs).

Diagnostic	Definition (words)	Example application(s) in EMLNs	Reference
Multiedge	A vector (whose length is equal to the number of layers) that consists of the set of edges that connect a given pair of nodes in different layers of a multiplex network.	Represent a set of ecological interactions between two species.	64
Multidegree	Total number of multiedges incident to a given node.	Quantify generality and/or vulnerability of a species across different interaction types, different places, etc.	64
Versatility	A generalisation of centrality measures that considers a node's importance across multiple layers.	Identify species that are important (i.e., versatile), because they bridge different interaction types, communities, and/or locations	65
Clustering coefficients	Measure extent to which nodes in a network tend to form transitive triples.	Evaluate the tendency of species to form interaction triples across sites or when there are multiple types of interactions.	66
Network community structure	Sets of nodes (in the same or different layers) that are connected to each other more densely than to other nodes in a network; network communities (i.e., modules) are usually identified as the output of an algorithm.	Identify modular structure across multiple times, spatial locations, and/or interaction types.	42,67,68
Stochastic block models	Generative statistical models to which one fits network data to find mesoscale features (such as modular structure, core-periphery structure, or others).	Identify sets of species across multiple times, spatial locations, and/or interaction types.	69,70
Node degree correlation across layers	Indicates relationship between intralayer degrees in different layers (e.g., are high-degree nodes in one layer typically also high-degree nodes in other layers?)	Are species generalists or specialists with respect to various interaction types or in various patches?	71
Reducibility	Find the layers needed to represent an ecological system in a way that would be distinguishable from an aggregated network?	(1) Guide for temporal and/or spatial resolution at which data should be collected. (2) In a network in which each layer is a different community, indicates which of the communities contain unique species and/or interactions. (3) Informs researchers about aggregation of data.	72
Participation coefficient and overlapping degree	Structural role that a node plays in the distribution of edges across layers (in the spirit of the roles of species in interconnecting communities ⁴).	Explore the functional role that species play in a community while considering several interaction types.	73
Node/interaction turnover	Mean proportion of node appearance and disappearance in different layers.	Understand the time-dependence of network structure and the temporal turnover rates of species.	8,74
Measures of beta diversity	Similarity between a pair of network layers due to differences in species and/or interactions.	Investigate how networks vary in space or time and link such variation to ecological factors such as distance between patches or species dispersal abilities.	21

See the references for explicit mathematical definitions. Many other diagnostics for, and other features of, multilayer networks can be found in refs. ^{13,14}

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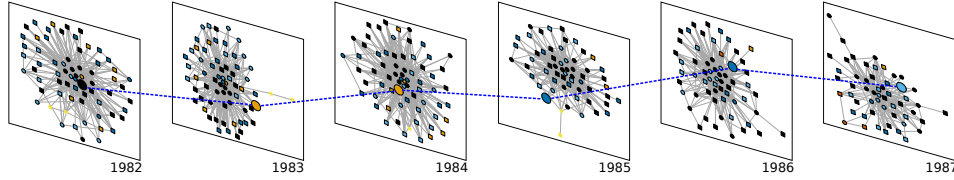
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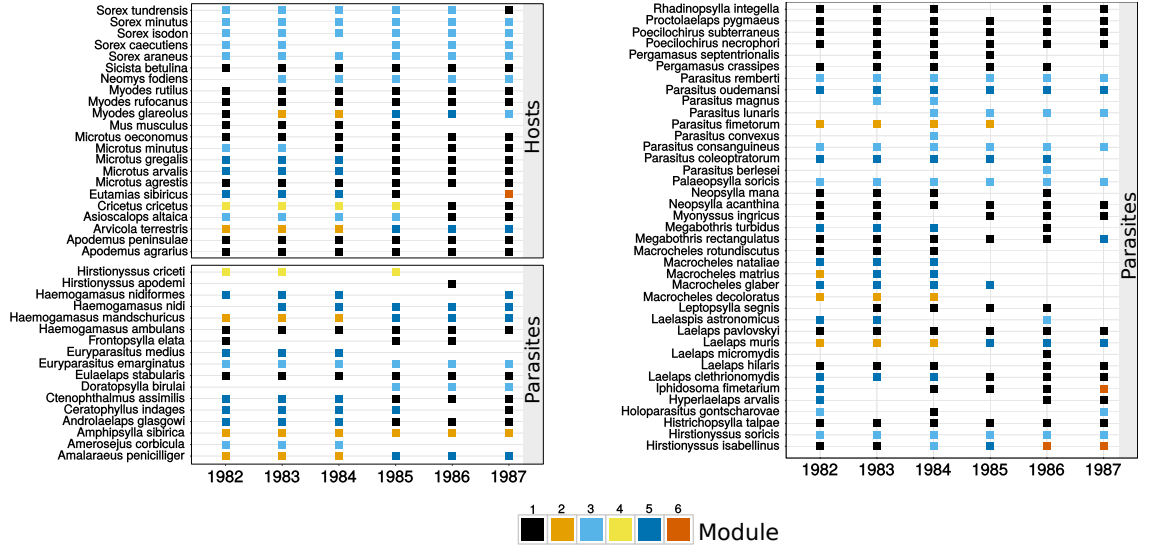
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Supplementary Information

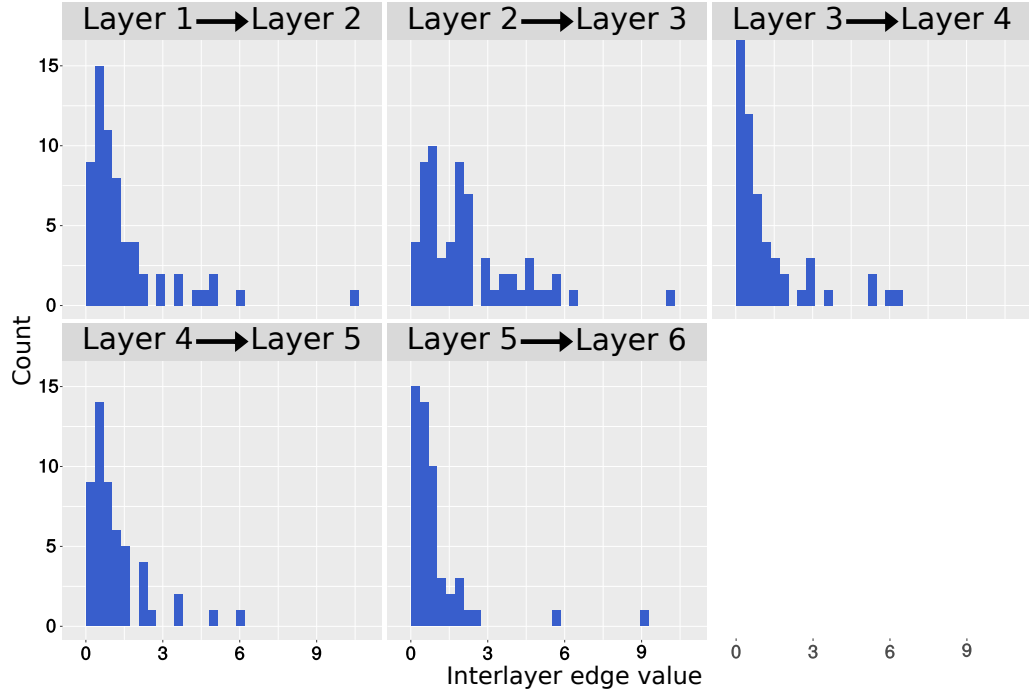
Supplementary Figures and Tables



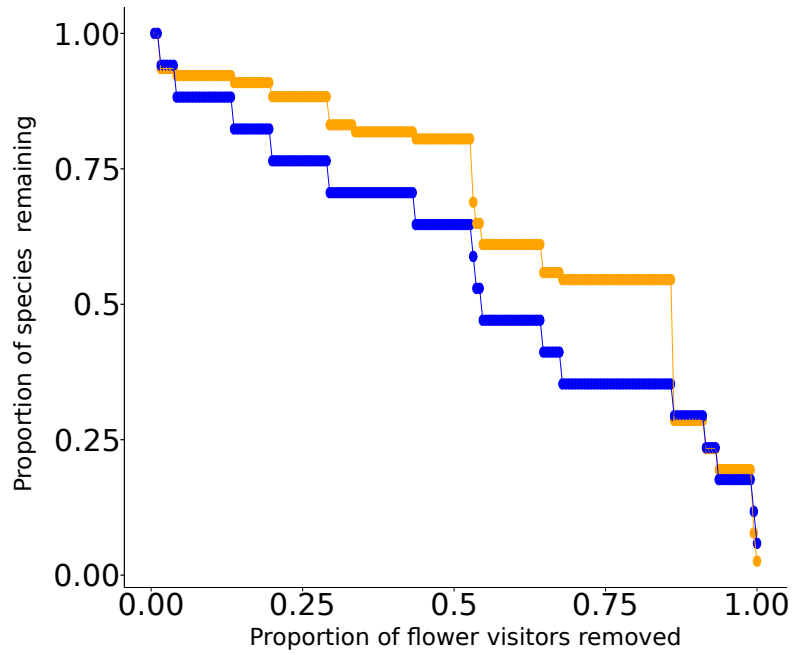
Supplementary Figure 1: Modules in a temporal network. The network represents infection of mammalian hosts (circles) by fleas and mites (squares) over 6 consecutive summers (6 layers). Intralayer edges represent the prevalence of a given parasite in a given host. Interlayer edges represent changes in species abundance between consecutive layers. For clarity, we show only one interlayer edge. We show different modules in different colours (we use the same colours in Supplementary Figure 2). For simplicity, we follow previous studies and assume that the intralayer and interlayer^{42,43} edges are undirected.



Supplementary Figure 2: Module affiliation of species across years for the host–parasite network analysed in the main text. We represent different modules using different colours. We show community assignments for a particular example (the one with the highest value of maximum modularity Q_B) among the 100 instantiations of applying the generalised Louvain algorithm⁷⁵ for multilayer modularity maximization. The figure illustrates that species can change their module affiliation across years. Missing data points indicate that a species is not present in a particular year.



Supplementary Figure 3: Distribution of the values of interlayer edges of the host-parasite temporal network. We calculate interlayer edge weights as the relative changes in abundance of a species during the time window $t \rightarrow t + 1$. Each histogram gives the distribution of values for a given time window of the network (there are 6 layers and hence 5 time periods). See the main text and Supplementary Note 3 for details on the calculation of interlayer edge weights.



Supplementary Figure 4: Network robustness to species removal for the plant–flower-visitors and plant–leafminer-parasitoids diagonally-coupled multilayer network. The curves indicate the proportion of (blue curve) surviving plants and (orange curve) surviving plants and parasitoids as a function of the proportion of flower visitors that have been removed. In each scenario, we remove flower visitors in the same order, which is by increasing intralayer node degree. (That is, we first remove the lowest-degree flower visitors, and we proceed accordingly.)

Supplementary Table 1: Types of ecological multilayer networks that have been examined and questions that can be addressed. In our list, we include studies that used multiple networks that were not explicitly connected to each other via interlayer edges.

Layer	Nodes	Interlayer edges	Intralayer edges	Structural characteristics	Primary research themes/questions	Reference	Figure
Time	S	Each node to itself (ordinal)	M, P, T	A set of networks defined separately at different time points.	Temporal variation in network or node diagnostics (e.g., centrality, connectance). Species and/or interaction turnover. Network-assembly dynamics. Temporal variation in beta diversity of species and/or interactions.	8,12,17,21,48,76-90	Fig. 2a
Space	S	Each node to itself (categorical)	M	A set of networks defined separately at different sites.	Spatial variation in network or node diagnostics (e.g., number of species, connectance). Spatial variation in beta diversity of species and their interactions as a function of geographic distance.	21-23	Fig. 2b
Interaction type	S, FA	Each node to itself	M, P, T, G	Networks interconnected via shared species (diagonal coupling).	How do different interaction types change understanding of ecological and evolutionary dynamics? How do different interaction types affect the stability and robustness of a system? What is the association between host immunogenetics and host-parasite interactions?	9,10,30,31,51,91	Fig. 2c
Interaction type	S	Each node to itself	T, P, NT+, NT-	Layers with the same set of species and different interaction types (e.g., parasitism, trophic, facilitation, mutualism) or signed networks.	Quantify architecture of trophic and non-trophic interactions, and quantify the association between these different interaction types. How does including different interaction types affect functional diversity and species roles? How are parasite transmission dynamics affected by different routes of transmission? How do invasive/migratory species affect the communities into which they arrive?	29,32,33,92,93	Fig. 2d
Community	S	Each node to itself	T	Food webs interconnected via common species.	How does interaction between food webs (via common species) affect the dynamics of each food web separately?	20,35	Fig. 2c
Community	S	Dispersal	M, T	Networks of communities (e.g., food webs, mutualistic bipartite networks) connected by species dispersal. The communities can be spatially embedded.	How are dispersal and colonization-extinction dynamics associated with network architecture in each community?	16,94-96	Fig. 2f
Multiple	I, P, C	Each node to a node in an adjacent level.	Sc, T, D	Network layers describe different hierarchical levels of the system.	How do processes at one level affect those in other levels?	39	Fig. 2f
Population	I	Each node to itself	Sc	Network layers defined separately for each behavioural interaction.	How are the function and dynamics of animal social networks defined by different behaviours?	97	Fig. 2d
Population	I	Between nodes from different layers	Sc	Layers interconnected through one or more nodes.	Disease dynamics in interconnected populations of different hosts.	34	Fig. 2e

Nodes: Species (S), Individuals (I), Communities (C), Metacommunities (MC), Functional alleles (FA). Intralayer edges: Mutualistic (M), Parasitism (P), Trophic (T), Non-trophic positive (NT+), Non-trophic negative (NT-), Genetic (G), Dispersal (D), Social (Sc). References are to studies that explored either networks with multiple but independent layers or multilayer networks with interlayer edges. The Interlayer column is relevant for studies that explicitly used interlayer edges, and it also indicates how the different layers in studies of multiple disconnected networks can be linked to each other. There may exist layer categories that we have not included.

Supplementary Table 2: Community structure of the host–parasite temporal network for three scenarios of interlayer edge weights.

Ecological Community	network type	Interlayer edge weights	\bar{Q}_B	Number of Modules (\bar{n})	Host adjustability, parasite adjustability
Layer 1	monolayer	0	0.46	6.47	N/A
Layer 2	monolayer	0	0.43	5.63	N/A
Layer 3	monolayer	0	0.40	6.22	N/A
Layer 4	monolayer	0	0.49	4.16	N/A
Layer 5	monolayer	0	0.35	4.49	N/A
Layer 6	monolayer	0	0.56	5.88	N/A
Whole network	multilayer	1000	0.99	2.96	0 , 0
Whole network	multilayer	Relative change in abundance	0.55	6.30	0.474 , 0.351

Each of the values of maximized modularity (\bar{Q}_B), the number of modules (\bar{n}), and the fraction of hosts and parasites that are assigned to more than one module (i.e., host and parasite adjustability, respectively) is a mean over 100 instantiations of the generalised Louvain algorithm^{42,75}. We adjust the null model in the multilayer modularity objective function from⁴² to make it suitable for bipartite networks. In monolayer networks, it is not possible to compare modules across layers without resorting to an ad hoc approach, so we place a value of N/A in the table. We use the interlayer edge weight $\omega = 1000$ for our calculations near the extreme case $\omega = \infty$.

Supplementary Table 3: Comparison of the observed host–parasite network with weighted intralayer and interlayer edges to three null models.

Reshuffled	\overline{Q}_B	Number of modules (\overline{n})	Host adjustability	parasite adjustability
None (observed)	0.55	6.3	0.474	0.351
Intralayer edges	0.41 ($P < 0.001$)	4.9 ($P < 0.001$)	0.372 ($P < 0.001$)	0.448 ($P < 0.001$)
Interlayer edges: hosts	0.21 ($P < 0.001$)	38.6 ($P < 0.001$)	1 ($P < 0.001$)	0.928 ($P < 0.001$)
Interlayer edges: parasites	0.21 ($P < 0.001$)	94.6 ($P < 0.001$)	1 ($P < 0.001$)	0.928 ($P < 0.001$)
Permuted order of layers	0.55 ($P \approx 0.52$)	17.1 ($P < 0.001$)	0.446 ($P < 0.001$)	0.395 ($P < 0.001$)

Each of the values of maximized modularity (\overline{Q}_B), the number of modules (\overline{n}), and the fraction of hosts and parasites that are assigned to more than one module (i.e., host and parasite adjustability, respectively) is a mean over 100 instantiations of the generalised Louvain algorithm^{42,75}. We adjust the null model in the multilayer modularity objective function from⁴² to make it suitable for bipartite networks. We calculate the p-values P (in parentheses) by comparing the mean of 100 instantiations of the observed network to 100 reshuffled networks.

Supplementary Table 4: Algorithms for the examination of network robustness to species extinctions.

Removal scenario	Algorithm	Ecological reason- ing/comments
Monolayer: Remove plants and follow parasitoids' secondary extinctions.	<ol style="list-style-type: none"> 1. Remove the plant with the lowest degree in the plant–parasitoid layer. 2. Remove all intralayer edges of the plant. 3. Remove any parasitoids in the layer that remain disconnected (i.e., have degree 0). 4. Record the proportion of surviving parasitoids in the layer as a function of the proportion of plants removed. 5. Repeat until all parasitoids are extinct in the layers. 	<ol style="list-style-type: none"> 1. Work only on the plant–parasitoid layer. 2. We use proportions, because it allows us to compare the different scenarios.
Multilayer: Remove flower visitors and follow parasitoids' tertiary extinctions.	<ol style="list-style-type: none"> 1. Remove the flower visitor with the lowest degree. 2. Remove all intralayer edges of the flower visitor. 3. Remove any plants in the layer that remain disconnected (i.e., have degree 0). 4. Remove any parasitoids that remain disconnected. 5. Record the proportion of surviving plants and the proportion of surviving parasitoids (separately) as a function of the proportion of flower visitors removed. 6. Repeat until all parasitoids are extinct in the layers. 	<ol style="list-style-type: none"> 1. A removal of a plant from the flower-visitor layer entails immediate removal of a plant from the parasitoid layer. 2. We use proportions, because it allows us to compare the different scenarios.
Multilayer: Remove flower visitors and follow parasitoids' tertiary extinctions; along with uniformly random plant removal	<ol style="list-style-type: none"> 1. Remove the flower visitor with the lowest degree. 2. Remove all intralayer edges of the flower visitor. 3. Remove any plants in the layer that remain disconnected (i.e., have degree 0). 4. Select a plant from the surviving plants uniformly at random and remove it with a probability of p_{rand}. 5. Remove any parasitoids that remain disconnected. 6. Record the proportion of surviving plants and the proportion of surviving parasitoids (separately) as a function of the proportion of flower visitors removed. 7. Repeat until all parasitoids are extinct in the layers. 	<ol style="list-style-type: none"> 1. Same as the previous scenario but incorporates a uniformly random plant extinction with probability p_{rand} (we consider examples with $p_{\text{rand}} = 0.3$ and $p_{\text{rand}} = 0.8$) to acknowledge the fact that extinctions can happen not only due to removal of flower visitors but also due to other processes that operate directly on plants. 2. Because of the random plant extinctions, we average results over 100 instantiations.

Supplementary Table 5: Available software for analysing multilayer networks

Software	Interface	Uses	Link
MUXVIZ ⁹⁸	Graphical user interface (but may require some knowledge of R and OCTAVE)	Visualization, interlayer correlations, network centrality, reducibility, modularity, node and edge statistics, motifs.	http://muxviz.net
MULTILAYER NETWORKS LIBRARY	PYTHON	Provides data structures for multilayer networks and basic methods for analysing them.	http://www.plexmath.eu/wp-content/uploads/2013/11/multilayer-networks-library_html_documentation/
GENLOUVAIN ⁷⁵	MATLAB	Code for examining network community structure in multilayer networks with diagonal coupling.	http://netwiki.amath.unc.edu/GenLouvain/GenLouvain ; in the SI, we include code (modified from the original) for the case in which layers are bipartite networks.
LOCALCOMMUNITYMATLAB		Local community-detection method used in ⁶⁷ .	https://github.com/LJeub/LocalCommunities
INFOMAP ⁶⁸	STANDALONE, WEB INTERFACE	Community structure detection using flow dynamics.	http://www.mapequation.org/code.html
BETALINK PACKAGE ^{21,99}	R	Quantify dissimilarity between ecological networks.	https://github.com/PoisotLab/betalink
TIMEORDERED PACKAGE ^{12,100}	R	Analyse temporal networks.	https://cran.r-project.org/web/packages/timeordered/index.html
MULTIPLY PACKAGE ¹⁰¹	R	Algebraic procedures for the analysis of multiplex networks. Create and manipulate multivariate network data with different formats.	http://cran.r-project.org/web/packages/multiplex/index.html

We specify websites to download the software. When relevant, we also include citations to associated references.

1 Multilayer Modularity Maximization

We use the multilayer modularity quality function $Q_{\text{multislice}}$ ⁴². Consider a (weighted or unweighted) unipartite multilayer network whose only interlayer edges are diagonal (i.e., interlayer edges only connect nodes to their counterparts across layers). With the standard (Newman–Girvan) null model, multilayer modularity is⁴²

$$Q_{\text{multislice}} = \frac{1}{2\mu} \sum_{ijsr} \left[\left(A_{ijs} - \gamma_s \frac{k_{is}k_{js}}{2m_s} \right) \delta_{sr} + \delta_{ij} \omega_{jsr} \right] \delta(g_{is}, g_{jr}), \quad (1)$$

where A_{ijs} is the weight of the intralayer edge between nodes i and j on layer s (for an unweighted network, the weight is exactly 1 if there is an edge), the tensor element ω_{jsr} gives the weight of the interlayer edge between node j on layer r and node j on layer s , the resolution-parameter value on layer s is γ_s , the quantity k_{is} is the intralayer strength (i.e., weighted degree) of node i on layer s (and k_{js} is defined analogously), $2m_s$ is the total edge weight in layer s , the set g_{is} is the community that contains node-layer (i, s) (and g_{js} is defined analogously), we denote the Kronecker delta between indices x and y by δ_{xy} (which is equal to 1 for $x = y$ and equal to 0 for $x \neq y$), and $2\mu = \sum_{ijs} A_{ijs}$. In an ordinal multilayer network (e.g., for the usual multilayer representation of a temporal network), ω_{jsr} is nonzero only when s and r are consecutive layers.

For our calculations, we need to adjust the null-model contribution $P_{ijs} = \gamma_s \frac{k_{is}k_{js}}{2m_s}$, which gives the expected number of interactions between nodes i and j in layer s , to consider the bipartite structure of a host–parasite network. That is, hosts are only allowed to be adjacent to parasites, and parasites are only allowed to be adjacent to hosts (see^{43,45,102} and some references therein for discussions of null models for multilayer modularity

maximization). To do this, we adapt Eq. (15) from Barber *et. al*¹⁰³ and write a bipartite multilayer modularity as

$$Q_B = \frac{1}{2\mu} \sum_{ijsr} \left[\left(A_{ijs} - \gamma_s \frac{k_{is} d_{js}}{m_s} \right) \delta_{sr} + \delta_{ij} \omega_{jsr} \right] \delta(g_{is}, g_{jr}), \quad (2)$$

where k_{is} is the strength of host i on layer s and d_{js} is the strength of parasite j on layer s . We modify the code from <http://netwiki.amath.unc.edu/GenLouvain/GenLouvain> (see Supplementary Table 1 and MATLAB code in the Supplementary Information) by changing the employed null model P_{ijs} . We use the default resolution-parameter value of $\gamma = 1$ ^{42,43}.

We maximize the quality function (equation (2)) using a generalized Louvain-like locally greedy algorithm⁷⁵ ((see⁴³ for details on the generalized Louvain algorithm and¹⁰⁴ for the original Louvain algorithm), which also determines module affiliation^{42,43}. As with all other algorithms for maximizing modularity and module composition in monolayer networks^{40,41}, the Louvain algorithm is a heuristic, and it yields a network partition that corresponds to a local maximum of modularity (and, importantly, we recall that the modularity landscape has a very large number of “good” local maxima)¹⁰⁵. It is also a stochastic algorithm, so different results tend to yield different module assignments and somewhat different modularity values. We thus average the values of the maximized modularity Q_B and the number n of modules across 100 instantiations of the algorithm and present results for the mean modularity \overline{Q}_B and mean number \overline{n} of modules.

The generalized Louvain algorithm⁷⁵ receives as input a modularity matrix, which is calculated according to the supra-adjacency matrix of a network (see Fig. 1b for an example of a supra-adjacency matrix and equation (2)). Given any supra-adjacency matrix that represents a diagonally-

coupled multilayer network, we have a viable input for optimizing multilayer modularity of that network. In the Supplementary Information, we present the code that we use for maximizing modularity and thereby assigning state nodes to modules. The output of one instantiation of the algorithm is a value for Q_B and an assignment of each state node to a module.

2 Analysis of a Synthetic Network with Two Interaction Types

The network in Fig. 3 has a ‘planted’ modular structure of 3 modules in each layer. We use a binary form of the network, in which intralayer edges have a value of 1 if they exist and 0 if they do not¹⁰. For simplicity, we assume that all interlayer edges have the same weight. To present the results of the optimization procedure, we report mean values $(\overline{Q}_B, \overline{n})$, averaged over 100 instantiations of the modularity-maximization algorithm, for the multilayer modularity Q_B and the number n of modules.

3 Analysis of a Temporal Network

3.1 Interlayer Edge Weights on a Comparable Scale as Intralayer Edges.

We examine a temporal network that encodes the infection of 22 small mammalian host species by 56 ectoparasite species (mites and fleas) during six consecutive summers in Siberia (1982–1987), giving 6 different layers (see refs.^{47,48} for more details on data). Not all species occur in all years. The data set also includes the number of host specimens collected in the field and the number of parasites recovered from each host specimen. We use

these individual-level estimates of host and parasite abundances, respectively, to determine the weights of intralayer and interlayer edges. The weight of an intralayer edge between host i and parasite j at time t is $A_{ijt} = m_{ij}^t = p_{ij}^t/a_i^t$, where A_{ijt} is the generic notation⁴² for an intralayer edge weight in layer t , the quantity p_{ij}^t is the number of parasite specimens of species j recovered from all of the specimens of host i at time t , and a_i^t is the number of specimens of host i at time t . The interlayer edge that connects host species i at time t to its counterpart at time $t+1$ has a weight of $\omega_{it,t+1} = n_i^{t \rightarrow t+1} = a_i^{t+1}/a_i^t$ given by the relative change in host abundance between the time points. An interlayer edge from node i in layer r to node i in layer s has weight ω_{irs} , where we have included a comma in the subscript between $r = t$ and $s = t+1$ for clarity and where we take $\omega_{irs} = \omega = \text{constant}$ in the synthetic network example. Analogously, the interlayer edge that connects parasite species j at time t to its counterpart at time $t+1$ has a weight of $\omega_{jt,t+1} = n_j^{t \rightarrow t+1} = p_j^{t+1}/p_j^t$ given by the relative change in the total abundance of the parasite (across all hosts). By definition, there is no interlayer edge between corresponding species in layers t and $t+1$ when (1) a species occurs in layer t but not in layer $t+1$ or (2) when a species does not occur in layer t but occurs in layer $t+1$.

The above formulation of edge weights is ecologically meaningful, as the weights reflect temporal dynamics in species abundances. It also allows one to model how changes in species abundances across time affect host-parasite interactions in each time point. For example, the future infection of a host i with parasite j depends on the interlayer edges and abundance values as follows:

$$m_{ij}^{t,t+1} = \frac{p_{ij}^{t+1}}{a_i^{t+1}} = \frac{p_{ij}^{t+1}}{n_i^{t \rightarrow t+1} a_i^t} = \frac{n_j^{t \rightarrow t+1} p_j^t}{n_i^{t \rightarrow t+1} a_i^t}. \quad (3)$$

Although we do not use the information in equation (3), it may be of inter-

est for other researchers interested in different questions. It gives nonzero weights to non-diagonal interlayer edges, which was done previously (and very effectively) for temporal networks of disease propagation in Valdano *et al.*¹⁰⁶.

It will also be instructive, for the sake of comparison with the two extreme scenarios $\omega = 0$ and $\omega = \infty$ (see Section 3.2), to indicate the numerical values of the weights of interlayer edges, which vary between 0.02 and 10.33. We show the distribution of the interlayer edge values in Supplementary Fig. 3.

For simplicity, in all of our calculations of the host–parasite temporal network, we follow previous studies and assume that the intralayer and interlayer^{42,43,107} edges are undirected. It will be interesting to relax this assumption in future studies of multilayer temporal networks with interlayer connectivity.

3.1.1 Testing Hypotheses About the Modular Structure

We now compare the modular structure in the observed network to that obtained from three different null models⁴⁴. For each null model, we test the hypothesis that the most modular partition of the observed temporal network is more modular than the most modular partition of reshuffled networks and calculate the significance of the modularity Q_B^{OBS} of the observed network’s most modular partition as the proportion of the 100 reshuffled networks that have a lower maximized modularity than that of the observed network¹⁰⁷. To obtain a more complete picture of modular structure, we also calculate the number of modules and the adjustability of hosts and parasites (the proportion of nodes of a given type that change modules at least once). Note that for comparative applications of adjustability one would

likely need to take the total number of temporal layers into account. We compare these results to the values that we obtain for the observed network using one-sample t -tests⁴⁴.

In the test with the first null model, we reshuffle the intralayer edges in each layer to test the hypothesis that modular structure over time depends on temporally-local interaction patterns. In each layer, we first reshuffle the total number of parasites that are on a given host. We use the `R0_BOTH` algorithm from the `VEGAN` package¹⁰⁸ in R. The algorithm shuffles the values and position of the matrix entries within each row, while preserving the total sum of the matrix. It therefore conserves both the number of parasite species that infect a given host and the mean abundance of those species. We then divide the matrix entries of each reshuffled matrix by the host abundance in that particular layer (i.e., year) to transform the abundance to prevalence values. We find statistically significant support for the hypothesis (see Supplementary Table 3). In addition, the observed network differs in a statistically significant way from the reshuffled networks with respect to both number of modules and host and parasite adjustability (see Supplementary Table 3).

In the second test, we reshuffle the interlayer edges between each pair of consecutive layers to test the hypothesis that the modular structure depends on the identity of hosts and parasites that change in abundance. To construct this null model, which is equivalent to the ‘nodal’ null model from⁴⁴, we separately permute the orders of node labels of hosts and parasites. We permute the node labels separately in each layer so that node identity is not preserved. In the bipartite networks, this is akin to permuting the order of rows (for hosts) or columns (for parasites) in each layer. We find that (1) the most modular partition of the observed network is more modular

than the most modular partition of the reshuffled networks (see Supplementary Table 3) and (2) their temporal structures differ. Specifically, the most modular partition of the observed network has approximately 6 times fewer modules than when reshuffling the order of hosts and approximately 15 times fewer modules than when reshuffling the order of parasites. In addition, in the reshuffled networks, almost all hosts and parasites switch modules at least once (see Supplementary Table 3).

In the third test, we permute the order of the layers to test the hypothesis that the order of time affects the network’s modular structure. To construct this null model, which is equivalent to the ‘temporal’ null model of⁴⁴, we draw a uniformly random permutation of the sequence $\{1, \dots, 6\}$ (e.g., $(4, 3, 2, 5, 1, 6)$) to give a new order of the layers. We thereby destroy the temporal identity of the layers. Note that the interlayer edges are not shuffled. We find that the most modular partition of the observed network is not more modular than the most modular partition of the randomized networks (see Supplementary Table 3), but that the observed and randomized networks have different temporal structures. The most modular partition of the observed network has about 2.5 times fewer modules than those of the randomized networks, and it also has different proportions of hosts and parasites that switch modules (see Supplementary Table 3).

3.2 Interlayer Edge Weights of 0 or Infinity

When maximizing multilayer modularity in a temporal network, one can examine the same scenarios as with the synthetic example. We compare the modular structure of the network with weighted intralayer and interlayer edges to the modular structure of two versions of the same network but in which interlayer edge values are set to either 0 or infinity. We perform

these computations in the same manner as we did for the interlayer-weighted network that we discussed in detail in Section 3.1. We again use same generalized Louvain algorithm from^{42,75}. To explore the scenario with infinitely large interlayer edge weights using numerical calculations, we set $\omega = 1000$. (Technically, we are thus approximate in our exploration of this extreme situation.) To explore the scenario with 0 interlayer edge weights, we examine 6 independent modularity matrices (corresponding to the 6 layers). We also provide the code for these computations.

Interlayer edge weights of infinity. As expected, when the weight of all interlayer edges is infinity, processes that govern interactions across contiguous layers (e.g., species persistence, survival, or changes in abundance) have a much larger effect on community structure than those that govern interactions within layers. Because the effect of species connectivity across time is much stronger than that of the intralayer processes, we can expect species to remain in the same module over time. In the limit of infinite-weight interlayer edges for all species, all state nodes that correspond to a given species must always be assigned to the same module. We find that setting interlayer edge weights to infinity results in the maximum value possible of $\overline{Q}_B = 1$, and the maximum-modularity partition of the network has $\overline{n} = 3$ modules. By construction, no species changes its module affiliation across time (see Supplementary Table 2).

Interlayer edge weights of 0. At the other extreme is a multilayer network in which all of the interlayer edges have a weight of 0, which is akin to maximizing modularity in each of the layers separately. In this case, the modules that one finds in different layers are independent of each other, as they reflect only the internal structure of each layer^{42,43}. This is the same

situation as calculating modularity for two disconnected networks in the toy example (see Fig. 3b). From an ecological perspective, one cannot understand the effect of interlayer phenomena (e.g., temporal changes in species abundance or in network topology) on modular structure in a direct manner if one has only 0 interlayer edge weights. Although some quantification of module evolution may be possible⁴⁶, such a quantification does not simultaneously encompass processes that occur within and between layers. For example, if a species interacts strongly with a given set of species in layer t but with another set of species in layer $t + 1$, one can argue that this is a change in the modular structure over time. However, even though it is possible, it need not be true, because the modules have been calculated independently for two distinct networks. Moreover, if a community splits in time, including nonzero interlayer edges provides a natural way to track which nodes leave to form a new community and which remain part of the original community.

When all interlayer edge weights are 0, we find that both $\overline{Q_B}$ and \overline{n} vary among the 6 layers (see Table 2 for exact values). Consequently, it is not possible to calculate changes in module composition (including host and parasite adjustability) in an unambiguous way, because modules are defined separately in a layer. One can, of course, attempt ad hoc analyses of modular structure changes in time even when interlayer edge weights are 0.

4 Further Details on Robustness Analysis

We use empirical data from Pocock *et al.*³⁰, who assembled a network composed of 10 layers, which are connected to each other (mostly) via plants. Layers in the original network include interaction of plants with granivo-

rous birds, rodents, butterflies and other flower visitors, aphids, granivorous insects and lead-miner parasitoids. For simplicity, we select a subset of the 10 layers and form a diagonally-coupled multilayer network with two layers. Our network describes two interconnected mutualistic interactions, although the mutualism in the leafminer-parasitoid layer is indirect. The network includes 189 flower visitors, 60 leafminer parasitoids, and 17 plants. For simplicity, we use a binary version of the original data. Pocock *et al.*³⁰ studied the effect of plant removal on the simultaneous co-extinction of the species that are interconnected to them. However, they did not study how disturbance percolates through plants, and they thus did not explore how the multilayer structure of the network affects cascading perturbations. In the context of our example, extinction of pollinators entails co-extinction of plants, and extinction of plants entails co-extinctions of leafminer parasitoids. Because an extinction of plants in one layer automatically implies their extinction in the second layer, we assume that the weights of interlayer edges are infinity. We modify an established algorithm of co-extinctions^{30,109} so that we can use it with multilayer networks (see Supplementary Table 4).

5 Additional Analysis of Robustness

We explore another option to compare the robustness of a monolayer network to that of a multilayer network. Unlike in the main text, we remove (in the same order) the same set of nodes (flower visitors) in the monolayer network and in the multilayer network, and we track the total proportion of species that remain in each of these networks. Specifically, in the monolayer network, we remove flower visitors in order of increasing degree and then compute the proportion of plants that remain. In the multilayer network, we remove the same flower visitors in the same order and then track the

proportions of both plants and parasitoids that remain. In the multilayer network, we find that the total proportion of surviving species is larger and that the pace of extinction is slower (see Supplementary Fig. 4).

Like standard simple approaches for studying network robustness⁵⁷, our calculations have the flavour of a percolation process (see Nagler *et al.*¹¹⁰ for an example of a percolation-based robustness study of an ecological multilayer network). Multilayer networks allow one to examine a much richer variety of percolation processes than in monolayer networks^{13,14,71}, and that in turn allows increasingly nuanced analyses of species robustness in ecological networks in a wealth of scenarios.

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